



## Small mammals taphonomy and environmental evolution during Late Pleistocene-Holocene in Monte Desert: The evidence of Gruta del Indio (central west Argentina)



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### ABSTRACT

Very few excavated sequences in southern South America provide an approximation to the environmental evolution covering the segment Late Pleistocene-Holocene. Here we present the taphonomic analysis and paleoenvironmental reconstruction based on the small mammal remains retrieved from the archaeological and paleontological site Gruta del Indio (Mendoza Province, Argentina). Radiocarbon dates situate the small mammal deposits studied within the Late Pleistocene and Holocene. Thus, these assemblages provide a record for inferring environmental evolution in the middle basin of Atuel River during the last ~31 ky BP. Taphonomic analysis revealed that most of small mammal remains were incorporated by a little destructive nocturnal owl. Recorded species include mainly cricetid and caviomorph rodents and a single marsupial. While Pleistocene assemblages have not exclusive species, the specific richness increases towards the Holocene probably linked with the climatic variability related to ENSO. In overall, the recorded small mammals suggest environmental stability during the Late Pleistocene-Holocene, mostly associated with Monte Desert conditions. Conversely, the pollen sequence studied from Gruta del Indio was interpreted as indicator of a deep environmental change during the Pleistocene-Holocene transition, when the Patagonian steppe was replaced by Monte Desert. Potential biases linked with these kinds of proxies are discussed.

### 1. Introduction

Taphonomy study the agents and processes involved in the transition of the organisms from the biosphere into the lithosphere (Efremov, 1940). Using actualistic parameters, the taphonomic study of micro-mammal remains recovered from both archaeological and paleontological sites provides evidence to infer the depositional and post-depositional agents implicated in the formation of the assemblages (e.g., Andrews, 1990; Fernández et al., 2017a and the references therein; Fernández-Jalvo and Andrews, 1992). Subsequently, this taphonomic knowledge can lead us to a more accurate interpretation of past environments (e.g., Andrews, 1990, 1995; Fernández et al., 2017a; Pardiñas, 1999a, 1999b; Terry, 2010).

Several small mammal fossil assemblages have been studied from localities now placed in the Monte Desert, one of the most arid environments of South America (e.g., Fernández, 2010; 2012a, 2012b;

Fernández and De Santis, 2013; Fernández et al., 2011a, 2011b, 2012, 2016a, 2016b; Ortiz et al., 2012; Pardiñas and Teta, 2013; López et al., 2018; Montalvo et al., 2016). This biome has micromammal species, both marsupials and rodents, well adapted to water stress and high diurnal temperatures, which have been studied from a variety of biological perspectives (e.g., Contreras and Rosi, 1980; Fernández, 2012a; Fernández et al., 2009a, 2017b; Gonnet and Ojeda, 1998; Novillo et al., 2017; Ojeda, 1989; Ojeda and Tabeni, 2009; Pardiñas et al., 2008, 2011, 2012, 2013; Roig, 1991; Rosi, 1983; Tabeni and Ojeda, 2003, 2005). However, very few excavated sequences with faunal remains in southern South America provide an approximation to the environmental evolution of Monte Desert covering the segment Late Pleistocene-Holocene (e.g., Fernández et al., 2011a, 2012; García, 2003a; Gil et al., 2011; Long et al., 1998; Martínez Carretero et al., 2013).

Archaeological and paleontological rockshelters in central south Mendoza Province are plenty of small mammal remains. Several of

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these deposits had been studied during the last two decades in order to produce new data for paleoenvironmental interpretations (e.g., Fernández, 2010, 2012a, 2012b, 2014; Fernández and De Santis, 2013; Fernández et al., 2009b, 2015a, 2015b; Gasco et al., 2006; Neme et al., 2002). Recently, an exhaustive search of the excavated materials at Gruta del Indio (GI, thereafter) and housed at Museo de Historia Natural de San Rafael (MHNSR, Mendoza, Argentina), revealed unstudied samples of faunal remains. Among them, the first fossil specimens of the endemic sigmodontine rodent *Holochilus lagigliai* (Lagiglia's marsh rat) were detected (Fernández et al., 2017b; Pardiñas et al., 2013). This marsh rat seems to be a mammal negatively affected by the growing pressure of humans on wetlands in the context of drylands that characterizes western Argentina (Fernández et al., 2017b).

GI is an emblematic archaeological and paleontological site located in the Monte Desert of CW Argentina. Several researches being conducted at this locality which provided a stratified sequence spanning the last ~31 ky BP (Lagiglia, 1956, 1968; Semper and Lagiglia, 1962–1968). GI has become one of the most important sources of evidence to infer the early human peopling of the CW Argentina and their controversial coexistence with Pleistocene megamammals (e.g., Borrero, 2002; Forasiepi et al., 2010; García, 1999, 2003a, 2003b; García and Lagiglia, 1999; Neme and Gil, 2008; Long et al., 1998).

Other relevant researches carried out in GI included palynological and paleoecological topics (Dacar et al., 2001; D'Antoni, 1983; García et al., 2008; Martínez Carretero et al., 2013). The analysis of the pollen sequence revealed a major environmental change around the Pleistocene-Holocene transition when the vegetation shifted from Patagonia to Monte. Apparently, this vegetational replacement was triggered by higher temperatures and increasing aridity, during Holocene times (D'Antoni, 1983). The pollen sequence studied in GI was taken as paleoenvironmental model for central south Mendoza Province (Markgraf, 1983; Zárate, 2002). However, other types of evidence from GI are not in agreement with pollen results. Plant remains contained in coprolites from small and medium rodents (cavids and chinchillids) as well as large-sized extinct equids (*Hippidium* sp.) suggested that Monte Desert conditions are settled since ~31 ka BP (Dacar et al., 2001; García et al., 2008; Martínez Carretero et al., 2013).

In this paper we present the taphonomic and taxonomic results of the study of the small mammal remains from GI. The formations of the deposits are evaluated and the paleoenvironmental conditions are inferred. Radiocarbon dates from GI indicate that the studied sequence constitutes a suitable record for inferring environmental evolution in the Monte Desert during the last ~31 ky BP.

## 2. Geographic and stratigraphic setting

GI is located close to the right margin of the Atuel River, 15 km S San Rafael in C Mendoza Province, Argentina (34°35' S, 68°22' W, 660 m asl, Fig. 1). The regional vegetation where GI is placed belongs to the Monte Desert (Abraham et al., 2009; Cabrera, 1976; D'Antoni, 1983), which is included in the climatic region known as the South American Arid Diagonal (Bruniard, 1982). It is exposed to the action of the Atlantic anticyclone, with a mean annual temperature about 15 °C and mean annual precipitation ca. 350 mm; precipitation is concentrated in summer. The vegetation of Monte is characterized by xerophytic shrubs such as *Larrea divaricata*, *Larrea cuneifolia*, *Cercidium praecox*, *Chuquiraga erinacea*, *Aloisia gratissima*, *Prosopis* spp., and isolated stands of *Geoffroea decorticans*, which grow in low organic matter sandy or rocky soils (Cabrera, 1976). Flood areas next to the river include herbs such as *Cortadeira speciosa*, *Phragmites australis* and *Typha subulata*. Communities of large dune fields are mainly composed by herbs such as *Panicum urvilleanum* and *Setaria mendocina* (Abraham et al., 2009; Roig et al., 2000). To the W and not far from GI, the regional landscape is characterized by large basaltic plateaus and volcanos allowing the northern penetration of Patagonian biotic elements (Fernández, 2012a; Roig et al., 2000).

GI is a large rockshelter (50 m wide at the mouth and 12 m long) that was eroded out of a basaltic outcrop, 20 m above the alluvial plain of the Atuel River. The sedimentary filling of GI is composed by about 1.1 m of gravel, sand, slime and archaeological materials (Semper and Lagiglia, 1962–1968). Small mammal samples come from 24 archaeological 2 m × 2 m squares (A7, B3, B6, B7, Ch-D2, Ch2, Ch3, D3, F2, F3, F4, F5, E2, E4, E5, H2, H8, Q6, Q7, R7, R8, S8, S9, T9); extracted sediments were sieved through 2 mm-sized mesh (Semper and Lagiglia, 1962–1968). General information of stratigraphy, chronology and cultural periods are presented in Table 1.

## 3. Materials and methods

### 3.1. Fossil samples

A total of 599 remains of small mammal were recovered from GI. Most of postcranial elements obtained from the sequence were discarded in the field by the collectors, following a widespread methodology mostly focused to the collection of remains that could be taxonomically identified. In this context, several taphonomic indices proposed by Andrews (1990) could not be applied on GI samples. The studied remains are assigned to the following temporal units: Layer 1 = ca. 2.3–1.9 ky BP (number of identified specimens (NISP) = 274; minimum number of individuals (MNI) = 98); Layer 2 = ca. 3.8–2.3 ky BP (NISP = 250; MNI = 126); Layer 3 = ca. 31–8 ky BP (NISP = 75; MNI = 34). In order to enlarge our perception of Late Holocene environments, a sample recovered from an open-air archaeological site named Rincón del Atuel 1 (RA-1, thereafter), located outside of GI, was used (Fernández, 2012a).

### 3.2. Modern sample

Paleoenvironmental reconstruction was supported on comparisons between both archaeofaunistic and modern micromammals assemblage derivate from owl pellet samples (e.g., Andrews, 1990; Fernández et al., 2017a). The latter used here was a large modern sample (N pellets [complete and fragments] = 165; MNI small mammals = 415) produced by *Bubo virginianus* (Magellanic horned owl) that was recovered from a nest inside the rockshelter (Fernández, 2012a; Fernández et al., 2009a).

### 3.3. Methods

Remains were observed under a stereomicroscope. Taxonomic identifications were made on cranial and dental remains, through comparisons against modern specimens belonging to the mammal collection of Museo de La Plata (UNLP, La Plata, Argentina) and specific literature (e.g., Fernández et al., 2011c; Pearson, 1995). Taxonomy follows here Patton et al. (2015). Since fragmentary remains of the caviomorph *Ctenomys* (tuco-tuco) and the cricetid *Eligmodontia* (silky mouse) are very difficult to identify at species level, they were characterized only to the generic level. Both archaeological and modern studied samples are housed in the MHNSR.

The categories of digestive corrosion (light, moderate, heavy and extreme) on teeth of rodents and marsupials were evaluated considering four categories of predators based on classification for small mammals from South America performed by Fernández et al. (2017a). The degree of the completeness of the skulls and mandibles was evaluated following Andrews (1990). Bone and teeth remains were identified following measures of taxonomic abundance and skeletal parts: NISP, MNE (minimum number of elements), MNI (Grayson, 1984). In addition, it includes an assessment of the relative abundance of skeletal elements proposed by Andrews (1990), that consider the representation of each one of them in the context of the MNI [MNEi/(Ei × MNI) × 100]. The studied samples of GI yielded the same values of NISP and MNE.

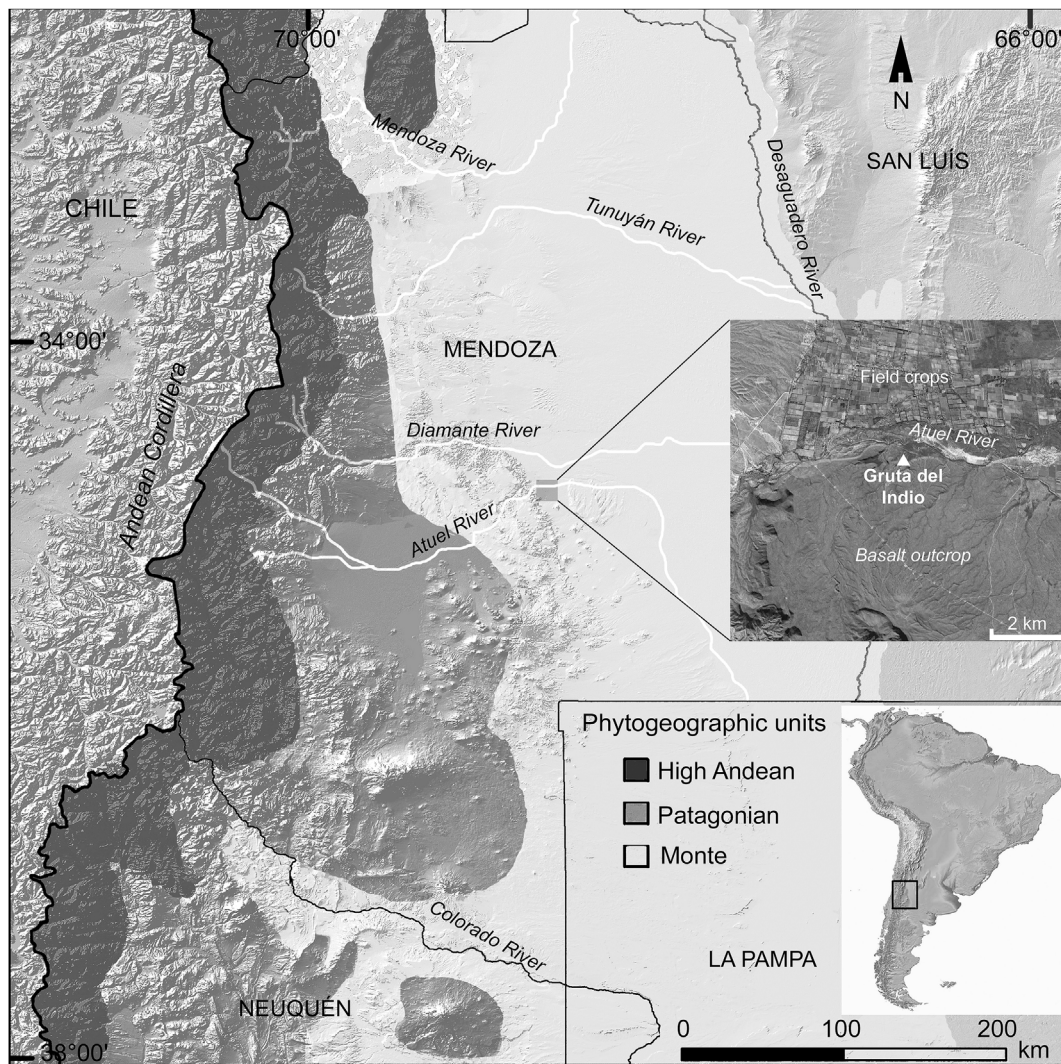


Fig. 1. Geographic location of the site Gruta del Indio in Mendoza Province, Argentina showing general topography and phytogeographic units (sensu Cabrera, 1976); in the inset, detail of the recent landscape around Gruta del Indio based on a satelital image.

Table 1

Gruta del Indio schematic sequence: stratigraphy, chronology and periods. Sources: Andreis (2007), García (1999, 2003a, 2003b), García and Lagiglia (1999), García et al. (2008), Lagiglia (1956, 1968), Long et al. (1998), Neme and Gil (2008), Semper and Lagiglia 1962–1968). Calibration was made using CALIB 6.0.1 program, in conjunction with Stuiver and Reimer (1993).

Depth in cm	Layers	Sedimentary composition	Main dates <sup>14</sup> C BP (lab code)	Calibrated age 2σ range BP	Approximate chronology	Cultural Periods
20–40	1	Yellowish brown loess	1910 ± 60 (GrN5397) 2210 ± 90 (GrN5493)	1689–1946 1945–2343	1.9–2.3 ky BP	Atuel II
40–100	2	Yellowish brown loess. Tephra band of 5 cm thick	2300 ± 60 (LP761) 3830 ± 40 (Gr-5395)	2109–2355 3984–4291	2.3–3.8 ky BP	Atuel III
70–110	3	Small fragments of basaltic rock fallen from the ceiling of the rockshelter	8990 ± 90 (LP925) 10,930 ± 540 (A1373) 24,140 ± 510 (LP1075) 30,800 ± 700 (LP918)	9734–10,241 11,223–13,896 27,974–29,945 33,974–36,728	8–11 ky BP 11–31 ky BP	Atuel IV – –
110–130	4	dark sand and gravel	–	–	–	–

Micromammals have been widely used as indicators of paleoenvironmental conditions since they are abundant and diverse in the archaeological and paleontological records. Most of these taxa have

relatively narrow environmental requirements, being frequently associated to particular microenvironments. Paleocological inferences are usually based on presence/absence of some species and/or relative

**Table 2**  
Preserved pellets, digestive corrosion, breakage in small mammal samples of Gruta del Indio, Mendoza, Argentina.

	Layer 1		Layer 2		Layer 3	
	N	%	N	%	N	%
Preserved pellet	1		0		0	
Specimens with hairs from pellets	18	6.6	12	4.8	4	5.3
Manganese oxide impressions	2	0.7	0	0	0	0
Burned specimens	6	2.2	19	7.6	2	2.7
<b>Digestive corrosion</b>						
Incisor digested	18	18	27	19.1	5	12.8
Molar digested	7	2.9	10	3.1	5	5.6
Femur digested	12	37.5	5	100	2	50
Humerus digested	4	22.2	0	0	0	0
<b>Breakage</b>						
Complete skull	2	4.5	3	5	0	0
Maxillary with zygomatic	17	38.6	14	23.3	4	22.2
Maxillary without zygomatic	25	56.8	43	71.7	14	77.8
Complete mandible	12	11.5	9	5.6	2	5.6
Mandible with ascendant ramus broken	37	35.6	58	35.8	12	33.3
Without ascendant ramus	38	36.5	79	48.8	16	44.4
Mandible with inferior edge broken	17	16.3	16	9.9	6	16.7
Broken femur	8	25	1	16.7	2	40
Broken humerus	5	29.4	1	100	1	100
Broken tibia	3	15.8	2	66.7	1	50
Broken ulna	0	0	0	0	0	0
Broken radius	0	0	0	0	0	0
Broken vertebra	0	0	10	76.9	0	0
Broken rib	1	100	0	0	0	0
Broken scapule	0	0	1	100	0	0
Broken pelvis	15	83.3	3	75	0	0
Broken autopodium	0	0	0	0	2	50

changes of its frequencies of MNI (e.g., Andrews, 1995; Fernández et al., 2012; Pardiñas, 1999a; Pardiñas and Teta, 2013).

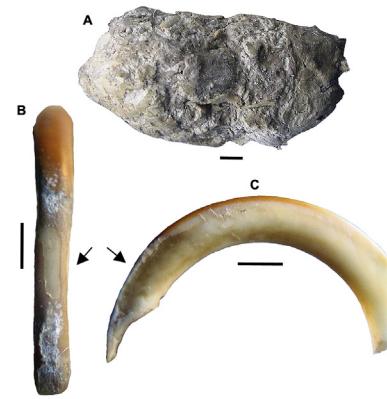
Taking into account the variation in samples sizes for the different archaeological and modern small mammal samples, rarefaction curves were calculated for each sample in order to assess reliability of richness and relative abundance of species in terms of MNI. Correspondence analysis was performed in order to explore species and samples ordination in multivariate space. This exploration was made on a data matrix of relative abundances (MNI%). Finally, the Shannon diversity index (H) was calculated for each sample based on MNI. Statistical analyses were made using the program PAST (PAleontological STatistics), version 3.12 (Hammer, 1999-2018).

## 4. Results

### 4.1. Taphonomy

Table 2 shows the main taphonomic attributes recorded in the studied samples from GI. One completed owl pellet was found in Layer 1 (Fig. 2a). In addition, several bones adhered to pellet debris were recovered throughout the stratigraphical sequence, although with the greatest incidence in Layer 1 (Table 2, Fig. 3a). Of the analyzed remains (femora, humeri and teeth), 8.5% showed signs of light digestive corrosion. Minor variations per layer (Layer 1: 7.4%, Layer 2: 9.2%, Layer 3: 9.4%) were found. In the proximal portions of the femora and distal portions of the humeri, 37.1% exhibited mark of light pitting. In the 17.8% of incisors the corrosion was concentrated on the edges (Fig. 2b and c). No teeth show the dentine affected by digestion. Only 3.4% of molars displays evidence of digestion. In Ctenomyidae and Octodontidae molars, the enamel surface showed slight pitting. In Caviidae molars, the occlusal corners are rounded and the salient angles are flattened. Cricetidae molars did not present signals of digestion.

Most of the bones (76.5%) were broken. Only 6.6% of cranial bones (skull and mandibles) were complete. The most frequent portions of skulls were maxillae without zygomatic arches (Table 2). The



**Fig. 2.** Examples of owl trophic activity at different layers of Gruta del Indio. A., Preserved pellet (Layer 1). B., Light corrosion in sigmoidontine incisor (Layer 2). C., Light corrosion in sigmoidontine incisor (Layer 3). Arrows indicates the enamel areas affected by corrosion. Scales = 2.5 mm.

mandibles presented different categories of breakage, with the highest proportion without ascendant ramus. Otherwise, most of the postcranial bones (66.5%) were complete. All broken bones presented sharp edges and rough surfaces.

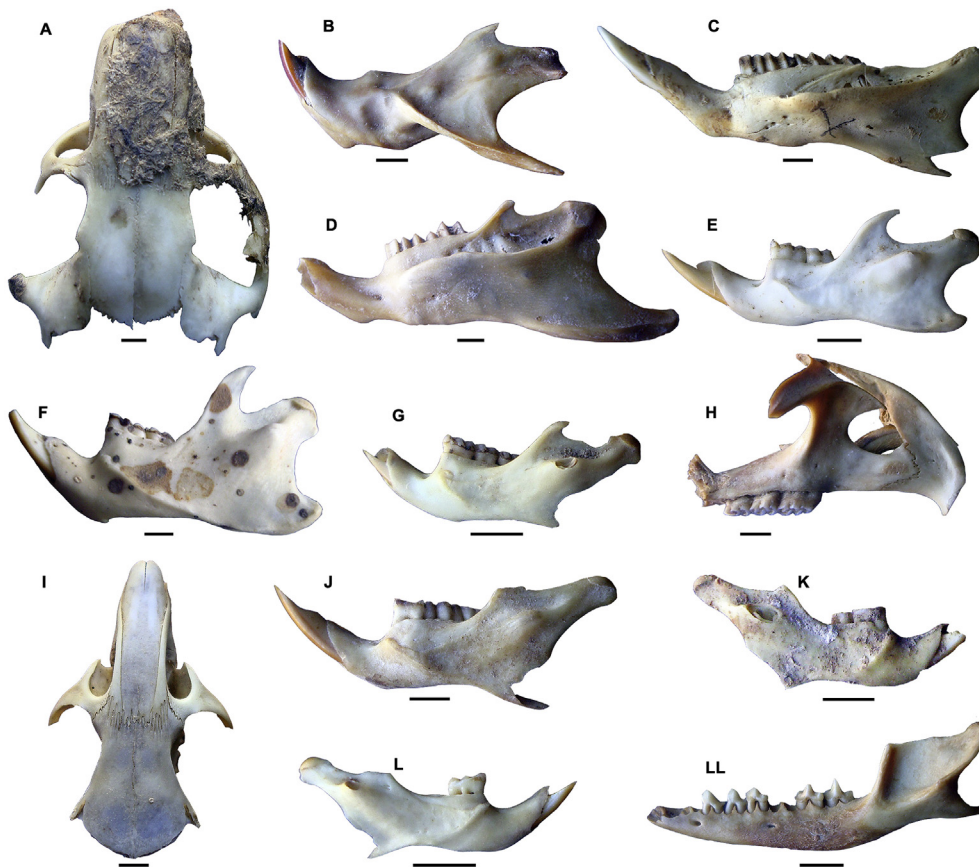
The anatomical representation indicated a high frequency of maxillae and mandibles, followed (mostly in Layer 1) by femora, tibiae, pelvis and humeri (Table 3). The average of the relative abundance was very low in all layers. This is because of the absence or very low presence of several postcranial elements (mainly autopodial), which could be associated to selection by the archaeologists while recovering the materials.

### 4.2. Taxonomic composition

The taxonomy and abundances of the small mammals recovered at GI are detailed in Table 4. In overall terms, samples are largely composed by caviomorph rodents, including two fossorial species, *Ctenomys* sp. and *Tympanoctomys barrerae* (plains viscacha rat) and the cavies *Microcavia australis* (southern mountain cavy) and *Galea leucoblephara* (lowland yellow-toothed cavy). Cricetid rodents are also an important component of the studied samples including eight sigmoidontines. The single marsupial recorded is the widespread didelphid *Thylamys pallidior* (mouse opossum) (Fig. 3).

Rarefaction analysis revealed that Layer 2 and modern owl samples reached an asymptote in clear contrast to the other assemblages studied (Fig. 4). This makes comparisons with layers 1 and 3, and RA-1 difficult due to while data from Layer 2 and modern owl sample provide a good representation of taxa richness, data from layers 1 and 3, and RA-1 may have been biased mostly by their small sample sizes.

Most of the small mammals are registered through the entire sequence. Four taxa were dominant with almost constant proportions (*Ctenomys* sp., *M. australis*, *G. griseoflavus* and *P. xanthopygus*). Five species were also constant through the sequence but in lower proportions (*T. pallidior*, *Eligmodontia* sp., *A. dolores*, *T. barrerae* and *G. leucoblephara*) (Table 4, Fig. 5). Four sigmoidontine species are exclusives for Late Holocene deposits (*C. musculus*, *R. auritus*, *H. lagigliai* and *O. flavescens*). The oryzomyines *H. lagigliai* and *O. flavescens* were restricted to the Layer 1 and Layer 2, respectively (Table 4). Four species are not represented in the modern owl sample (*H. lagigliai*, *R. auritus*, *T. barrerae* and *G. leucoblephara*). In line with these findings, correspondence analysis result (Fig. 6) shows all GI archaeological samples grouped, but modern owl sample did not, considering the main factor (Axis 1, 75.8% of the total variance).



**Fig. 3.** Small mammals recovered at Gruta del Indio. A., *Ctenomys* sp., fragmented skull in dorsal view showing pellet remains (Layer 1). B., *Typanoctomys barrerae*, left dentary in labial view (Layer 1). C., *Microcavia australis*, fragmented left dentary in labial view (Layer 3). D., *Galea leucoblephara*, left dentary in labial view (Layer 1). E., *Akodon dolores*, left dentary in labial view (Layer 1). F., *Holochilus lagigliai*, left dentary in labial view (Layer 1). G., *Oligoryzomys flavescens*, fragmented left dentary in labial view (Layer 2). H., *Reithrodon auritus*, right premaxillary and maxillary in lateral view (Layer 2). I., *Graomys griseoflavus*, fragmented skull in dorsal view (Layer 1). J., *Phyllotis xanthopygus*, fragmented left dentary in labial view (Layer 1). K., *Eligmodontia* sp., fragmented right dentary in labial view (Layer 2). L., *Calomys musculus*, fragmented right dentary in labial view (Layer 2). LL., *Thylamys pallidior*, fragmented left dentary in labial view (Layer 2). Scales = 2.5 mm.

**Table 3**  
Minimum number of elements (MNE) and relative abundances (Rel ab) in the small mammal assemblages from Gruta del Indio.

	Layer 1		Layer 2		Layer 3	
	MNE	Rel ab	MNE	Rel ab	MNE	Rel ab
Maxilla	44	22.4	60	23.8	18	26.5
Mandible	104	53.1	162	64.3	36	52.9
Isolated incisors	2	0.5	0	0	0	0
Isolated molars	5	0.4	0	0	1	0.2
Vertebra	28	0.9	13	0.3	6	0.6
Ribs	1	0.1	0	0	0	0
Scapula	0	0	1	0.4	0	0
Humerus	17	8.7	1	0.4	1	1.5
Ulna	3	1.5	0	0	1	1.5
Radius	1	0.5	0	0	0	0
Pelvis	18	9.2	4	1.6	3	4.4
Femur	32	16.3	6	2.4	5	7.4
Tibia	19	9.7	3	1.2	2	2
Calcaneus	0	0	0	0	1	1.5
Astragalus	0	0	0	0	0	0
Metapodial	0	0	0	0	1	0.1
Phalange	0	0	0	0	0	0
<b>Total</b>	<b>274</b>		<b>250</b>		<b>75</b>	
<b>Average</b>		<b>7.2</b>		<b>5.6</b>		<b>5.8</b>

None of the studied specimens showed signs of weathering, rodent marks, hydraulic transport and root action. Only two specimens of Layer 1 exhibited impregnation with manganese oxides.

## 5. Discussion

### 5.1. Taphonomy

Predation is one of the most recurring causes of small mammal

accumulations in both archaeological and paleontological cave sites, and digestive corrosion is their greatest evidence (e.g., Andrews, 1990; Fernández et al., 2017a, and references therein). Therefore, considering the biases in the recovery of GI small mammal remains, the interpretation of the causes of their deposition was cemented mainly on digestive corrosion.

The absence of cut-marks and the few burned remains detected in GI suggest mainly non-human deposition (Fernández et al., 2017c, and references therein). The finding of pellets and bones with adhered pellet debris throughout the entire sequence, light digestive corrosion on low percentage of teeth and postcranial bones are in agreement with an accumulation produced by owls (Andrews, 1990; Pardiñas, 1999b; Fernández et al., 2017a). *Tyto alba* (barn owl), *B. virginianus* and *Athene cunicularia* (burrowing owl) are the most common owls that inhabit the study area. *A. cunicularia* and *B. virginianus* yield accumulations with higher degree and proportions by digestive corrosion than *T. alba* (e.g., Andrews, 1990; Gómez, 2007; Montalvo and Tejerina, 2009; Montalvo et al., 2016). *T. alba* usually nests in caves and rockshelters, inhabits open landscapes and displays an opportunistic trophic behavior, feeding mostly on nocturnal small mammals (Andrews, 1990; Pardiñas, 1999a; Taylor, 2004). Most of the small mammal species recorded at GI are within the prey size range of this owl (Bellocq, 2000; Leveau et al., 2006).

The small mammal assemblages from GI are characterized by the absence of weathering, rodent marks, hydraulic transport, root action, as well as a very low frequency of bones with impregnation of manganese oxides triggered a good preservation and a rapid deposition in the stratigraphic context (Korth, 1979; Andrews, 1990). Nonetheless, the breakage of cranial and postcranial elements with sharp edges and rough surfaces indicates trampling action, a common taphonomic process at cave or rockshelter sites (Andrews, 1990; Pardiñas, 1999a, 1999b).

**Table 4**

Taxonomic composition (expressed NISP and MNI) and Shannon diversity index (H) of the small mammal sample from the archaeological sites Gruta del Indio (Layers 1, 2 and 3) and Rincón del Atuel 1 (RA-1; all component pooled), and modern pellet sample of *Bubo virginianus* from Gruta del Indio. \*Only postcranial elements, possibly corresponding to identified taxa.

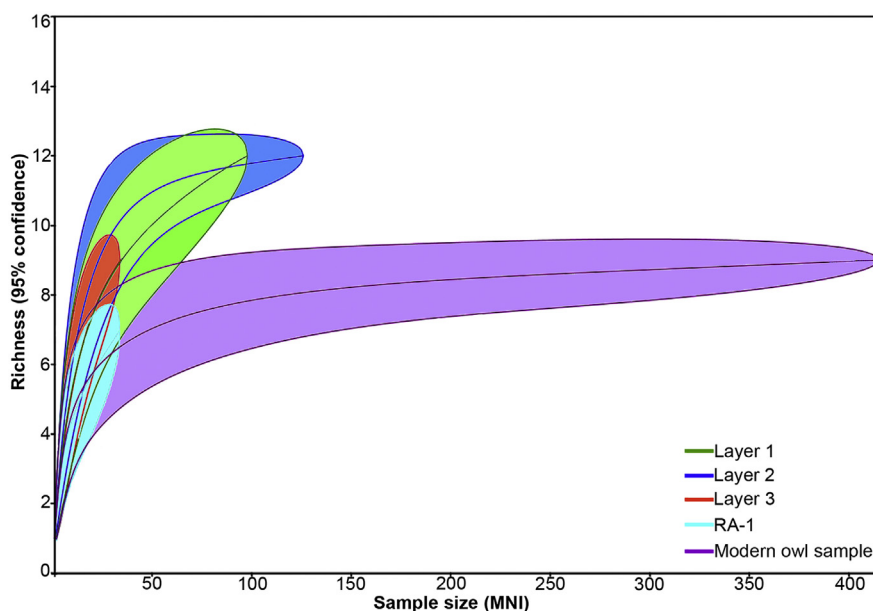
	Layer 1		Layer 2		Layer 3		RA-1		Modern sample
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	MNI
<b>Mammalia</b>									
<b>Didelphimorphia</b>									
<i>Thylamys pallidior</i>	1	1	12	7	2	1	1	1	56
<b>Rodentia</b>									
<b>Ctenomyidae</b>									
<i>Ctenomys</i> sp.	59	34	61	35	23	15	34	10	7
<b>Octodontidae</b>									
<i>Tympanoctomys barrerae</i>	12	8	19	11	6	2	0	0	0
<b>Caviidae</b> indet.*	50		11		12		109		
<i>Galea leucoblephara</i>	3	2	9	7	2	1	7	6	0
<i>Microcavia australis</i>	10	8	16	10	6	4	25	12	5
<b>Cricetidae</b> indet.*	69		17		8		53		
<i>Akodon dolores</i>	4	2	7	5	1	1	0	0	17
<i>Graomys griseoflavus</i>	35	21	51	22	7	4	3	3	73
<i>Phyllotis xanthopygus</i>	13	9	17	11	3	3	1	1	22
<i>Calomys musculus</i>	1	1	9	5	0	0	0	0	97
<i>Eligmodontia</i> sp.	9	6	16	9	5	3	1	1	137
<i>Reithrodon auritus</i>	1	1	4	3	0	0	0	0	0
<i>Holochilus lagigliai</i>	7	5	0	0	0	0	0	0	0
<i>Oligoryzomys flavescens</i>	0	0	1	1	0	0	0	0	1
<b>Total</b>	274	98	250	126	75	34	234	34	415
<b>Diversity (H)</b>		1.95		2.18		1.77		1.56	1.70

5.2. Paleoenvironments

The micromammal assemblages recorded in GI point to the persistence of open environments mostly composed by a shrubby steppes combined with large rocky outcrops since Late Pleistocene to Late Holocene. Biogeographically, rodents and marsupials in past and present samples from GI are reflecting Monte Desert biome typically linked to drier and warmer conditions (Abraham et al., 2009; Fernández, 2012a; Pardiñas et al., 2008).

A remarkable fact of the studied GI assemblages is that a pool of sigmodontine rodents mostly associated with Patagonia biome not

reached the site during the temporal segment represented. Today, about 100 km W GI, small mammal communities are typified by several Andean and Patagonian sigmodontine rodents such as *Loxodontomys micropus* [southern pericote], *Paynomys macronyx* [Andean long-clawed mouse], *Abrothrix olivacea* [olive grass mouse], *Abrothrix hirta* [long-haired grass mouse], *Euneomys mordax* [biting chinchilla mouse], *Euneomys petersoni* [Peterson's chinchilla mouse], plus the marsupial *Lestodelphys halli* (Fernández, 2012a; Pardiñas et al., 2008). The absence of all these species in GI is eloquent about the scarce change in micromammal assemblages during the last 31 ky. Interestingly, the Holocene small mammal records from Patagonian environments of S



**Fig. 4.** Rarefaction analysis for fossil samples of Gruta del Indio (Layers 1, 2 and 3) and Rincón del Atuel 1 (RA-1; all component pooled), and modern owl sample from Gruta del Indio. For all samples, 95% confidence intervals are shown.

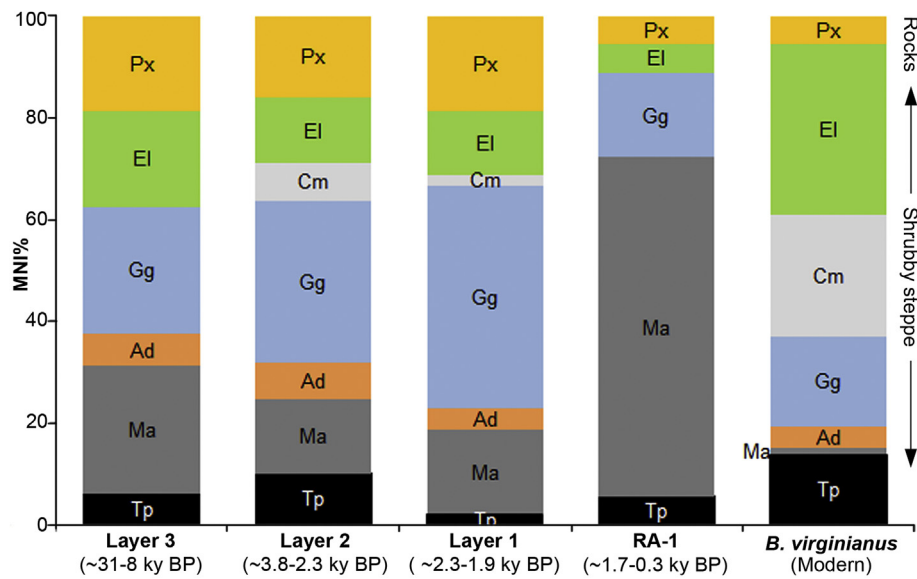


Fig. 5. Temporal changes in the relative abundance of some characteristic small mammal species in Gruta del Indio (Layers 1, 2 and 3), Rincón del Atuel 1 (RA-1; all component pooled) and modern owl samples from Gruta del Indio. References: Ad: *Akodon dolores*, El: *Eligmodontia* sp., Cm: *Calomys musculus*, Gg: *Graomys griseoflavus*, Ma: *Microcavia australis*, Px: *Phyllotis xanthopygus*, Tp: *Thylamys pallidior*.

Mendoza Province did not yield species allied to Monte Desert (Fernández, 2012a; Fernández et al., 2015a, 2015b).

Terry (2010) found out that past death small mammal assemblages reflect similar ecological structure of the modern communities; and that the effects of time-averaging on the increase of richness and diversity of species become significant at large time scale (hundreds to thousands of years). This represents an acceptable tool to interpretate environmental changes, including recent ones such as the Medieval Climatic Anomaly (MCA), the Little Ice Age (LIA) and the El Niño-Southern Oscillation (ENSO). Despite the remarkable taxonomic homogeneity displayed by GI small mammal sequence, the moderate increasing of richness and diversity in Late Holocene assemblages (Table 4), points out the

possibility of minor environmental variations during this segment. This scenery has been reported for small mammal assemblages from other regions, including Monte Desert areas, such as the nearest Cueva Huenul 1 (N Neuquén Province; ~16.6–0.4 ky BP), where took place a more heterogeneous environment since Early Holocene and up to the Late Holocene, including a mosaic of shrubby steppes, open bare areas, and large rocky outcrops (Fernández et al., 2011a, 2012). The findings of *O. flavescens* and *R. auritus* in layers 1 and 2 of GI could be associated to the development of body of water and herbaceous steppe (Fernández, 2012a; Pardiñas et al., 2008), suggesting a change to a bit more cooler and humid conditions, possibly associated with the interannual climate variability of ENSO (e.g., Zárate, 2002; Zárate et al., 2010).

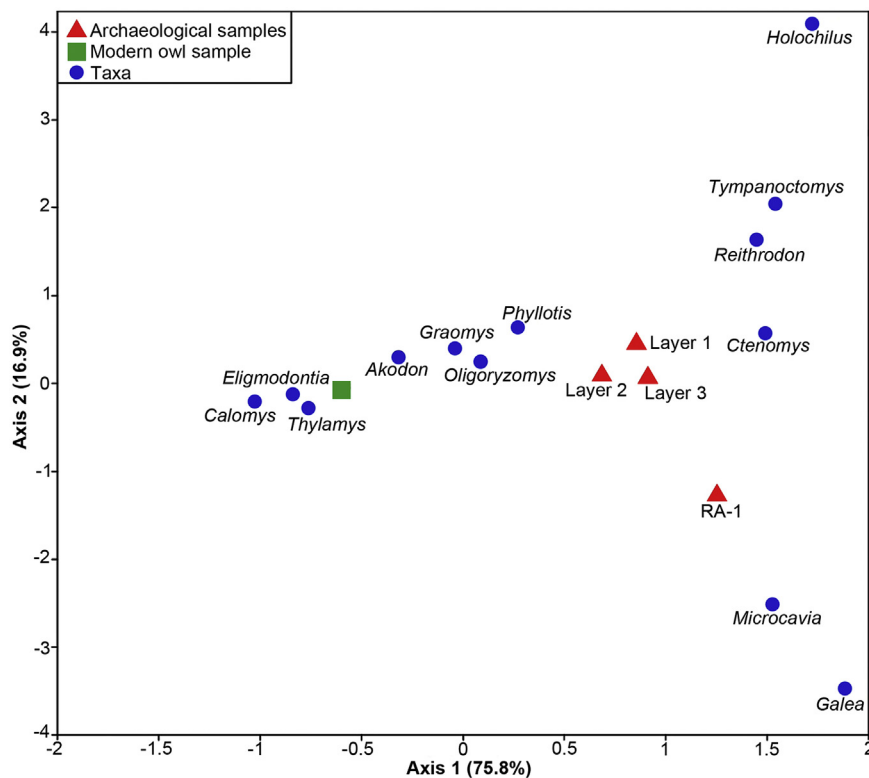


Fig. 6. Correspondence analysis of small mammal fossil assemblages from Gruta del Indio (Layers 1, 2 and 3) and Rincón del Atuel 1 (RA-1; all component pooled) and modern owl pellet samples from Gruta del Indio. Percentages of both axes show the variance.

The major change affecting small mammals that can be learned from GI sequence is the apparent extirpation of several species in the modern community. The sigmodontines *R. auritus*, and *H. lagigliai* and the caviomorph *T. barrerae* are not recorded today, suggesting local extirpations. In addition, the abundance of the fossorial rodent *Ctenomys* declines towards the recent and the opportunistic sigmodontines *Eligmodontia* sp. and *C. musculinus* dramatically increases (Fig. 5). Preliminary, this community reworking can be connected with the extensive environmental change that the area near GI suffered in the last centuries (Fernández, 2014). Among the human-made transformations developed there is the almost total conversion of the alluvial plain of the Atuel River to agroecosystems (Fig. 1). Natural vegetation was drastically reduced to a narrow fringe along the fluvial course (Roig et al., 2000). However, after the construction of the El Ñihuil dam, about 50 km SW GI, the river flooding regime was totally altered favoring the developing of wetlands and pounds (Fernández et al., 2017b).

The sharp contrast between past and present small mammal communities detected in GI was also recorded in several similar archaeological sequences in arid Argentina. Local and regional extirpations of rodents and marsupials—for example, the caviomorph *Tympanoctomys* and the marsupial *Lestodelphys*—are extensively recorded at 70 km S GI (Fernández, 2010), and Central and North Patagonia (Fernández et al., 2016b; Pardiñas et al., 2012). In the same region, the impoverishment of assemblages is also associated with the dramatic increment of opportunistic sigmodontines such as *C. musculinus* (Pardiñas et al., 2000). Late Holocene sequences in northwestern Argentina display similar modifications apparently linked to human action on the natural environments (Ortiz and Pardiñas, 2001; Ortiz et al., 2012). In line with these findings, other fossil records of small mammals located in Monte Desert showed great taxonomic stability through their sequences, although with deep changes in modern assemblages (Fernández, 2010, 2012a; Fernández and De Santis, 2013; Fernández et al., 2011a, 2011b, 2012, 2016a, 2016b; Ortiz et al., 2012; Pardiñas and Teta, 2013). In this context, the impact of recent climatic events, such as ENSO, MCA LIA, has been expressed as minor variations in the frequencies of some taxa and/or in the expansion/retraction of others (e.g. Fernández et al., 2011b; Ortiz et al., 2012).

### 5.3. Climatic stability or proxy limitations?

Small mammals studied in GI suggest a general stability of Monte conditions with some minor variations since Late Pleistocene to recent times. This inference is in sharp contrast with those derived from the study of the pollen sequence of GI. According to this proxy, a main environmental change took place between 12 and 10 ky <sup>14</sup>C BP, when the Patagonian steppe was replaced by Monte Desert as consequence of the implantation of warmer and drier conditions. Since Early Holocene to Late Holocene the Monte vegetation and the level of the Atuel River were gradually increased generating an expansion of the riparian forest mostly composed by *P. flexuosa* and *C. praecox* (D'Antoni, 1983; Markgraf, 1983). This paleoenvironmental pollen-model of GI was consistent with later pollen, sedimentological, malacological and glaciological studies performed in other parts of Mendoza Province (e.g., Zárate, 2002; Zárate et al., 2010, and references therein). However, in the northern part of this Province, the Late Pleistocene-Holocene stable isotopes ( $\delta^{13}\text{C}_{\text{OM}}$ ) and pollen studies of the Arroyo La Estacada were coherent suggesting that the alluvial deposits were mostly composed by local vegetation, with low occurrence of regional C<sub>4</sub> (Monte) and C<sub>3</sub> (Patagonian) plants communities, but with C<sub>4</sub> values increased at the Pleistocene-Holocene transition, and a mixture of C<sub>4</sub> and C<sub>3</sub> values during the last 4–3 ky, similar than today (e.g., Rojo et al., 2018, and references therein).

In this context, if Patagonian conditions characterized latest Pleistocene, as pollen reflects, why the local assemblage of micromammals transpires Monte conditions? The first point to address is how

accurate is the small mammal record of the Late Pleistocene in GI as indicator of environmental conditions. Although radiocarbon dates retrieved from Layer 3 are in agreement with stratigraphy, the fact that the temporal segment 31 to 10 ky is contained in less than 0.5 m of excavated sediments reflects condensation. We have no original data to interpret if micromammal remains were distributed across the entire layer or concentrated to the bottom, or to the middle or to the top. In this context, we can conclude that the Late Pleistocene studied sample is poor, limiting our interpretation of environmental conditions. However, no a single remain of rodents or marsupials denoting Patagonian environments was retrieved from this layer and, by the contrary, the elements recorded point to Monte environments. In NW Patagonia and S Mendoza Province at Patagonian and Monte Desert phytogeographic units, a hypothesis of the resilience of micromammal communities to minor or moderate climate-environmental changes was proposed in order to explained the taxonomic stability during the last 16 ky (Fernández et al., 2011a, 2012, 2015a, 2015b, 2016a; Pardiñas and Teta, 2013).

The results about environmental evolution as depicted by small mammals in GI are coincident with those inferred by others lines of evidence yielded in the same site. Plant remains extracted from coprolites of the rodents Caviidae (unidentified genera and species) and *L. viscacia*, and the extinct equid *Hippidium* sp. show elements of Monte Desert between 31 and 24 and ~9 <sup>14</sup>C ky BP (Dacar et al., 2001; García et al., 2008; Martínez Carretero et al., 2013). Could this agreement between small mammals and plant remains from faeces reflecting local conditions against those derived from pollen rain indicative of regional ones? Certainly, as we mentioned earlier, samples derived from owl pellets are representing local communities (Terry, 2010). Estimated home ranges for *T. alba* vary ca. 2 to 0.2 km<sup>2</sup> (e.g., Taylor, 2004; Thomsen et al., 2014) while *B. virginianus* preys even in smaller spaces (< 500 ha; see Bennett and Bloom, 2005). Taking in mind these restrictions, GI small mammal samples can be interpreted as representing the local community in a circle around the site of about 1 km in radius. Even suffering a regional change in environment conditions, the resilience of a local community could be sufficient strong to reflect an artefactual environmental stability. GI is open to the alluvial plain of the Atuel River, constituted by sandy lowlands. This kind of landscape favors penetration of Monte Desert vegetation.

The contrast between pollen and small mammals can not be solved solely with the evidence of GI at hand. More in general, the available data for Late Pleistocene micromammal communities from western Argentina is so scarce that any hypothesis is still venturate. In SW Neuquén Province, a sharp difference between Late Pleistocene and Holocene rodent assemblages was detected in Arroyo Corral archaeological and paleontological locality (Tammone et al., 2014). However, the Late Pleistocene-Holocene record of Cueva Huenul 1 shows a smooth transition without any clear sign of faunal replacement (Fernández et al., 2011a, 2012). It is important to remark that a chronological factor could be responsible for the observed differences between both mentioned records. While the Late Pleistocene assemblages of Arroyo Corral are dated around Last Glacial Maximum (LGM), those of Huenul cave are well inside postglacial times (~16.6–10 ky BP). At the onset of the LGM—between 24 to 18 ky—it is easy to imagine that Andean and piedmont biotic communities were hardly impacted due to their proximity to the ice front. However, a few thousands of year later glacial or periglacial were rapidly recolonized from lowland refuges (e.g., Pardiñas et al., 2011).

## 6. Conclusion

Taphonomical analysis pointed out that most of small mammals recovered at the emblematic archaeological and paleontological site GI were incorporated by a little destructive owl, possible *T. alba*. In addition, the small mammal assemblages had a good preservation and rapid incorporation in the stratigraphy sequence, although previously



exposed to trampling action. This taphonomic context ensures an appropriate framework for comparing with modern owl pellet samples, in order to carry out paleoenvironmental inferences.

Most of the small mammals registered throughout the stratigraphical sequence of GI are allied to shrubby steppe of Monte Desert. There are no small mammals exclusive for Late Pleistocene. Some new species are added at Holocene time, which could be associated to the climatic variability of ENSO. Some species from Late Pleistocene and Holocene never reached recent times, likely by the human impact which occurred in the last two centuries.

In sum, the taxonomic data provide no evidence of significant changes, despite the occurrence of the LGM during 24–18 ky BP, and the Pleistocene-Holocene transition. The micromammalian evidence is broadly coincident with those inferred by the analysis of coprolites of mammals performed in the same site. However, the pollen fossil record of GI and from nearby areas suggests a major environmental change during the Pleistocene-Holocene transition, when the Patagonian steppe was replaced by Monte Desert. The possibility of a discrepancy between proxies due to their specific responses to local and regional environmental-scale can not be ruled out.

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